PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.

PAPERS.

1. Coat Colour in Greyhounds.

By Adair Dighton, F.R.C.S., F.Z.S.

[Animal Breeding Research Department, University of Edinburgh.]

[Received October 13, 1922: Read February 6, 1923.]

Some months ago, my friend Mr. J. R. Robertson, knowing that I was interested in both the problems of Heredity and in Greyhounds, suggested that I should make extractions of their various coat colours from the stud books, and tabulate them on a definite plan with a view to ascertaining whether the results accorded with Mendelian principles and with previous data obtained by him from direct experiment. At the time Mr. Robertson suggested this, I was too busy with other affairs to undertake it, but at the end of the last coursing season I began what has been a hard but fascinatingly interesting work.

By way of preface, I should explain that the National Coursing Club is the ruling body in the coursing world, and under its direction the Greyhound Stud Book is issued annually. A rule of the Club stipulates that every litter of greyhounds must be registered within two months of the date of whelping, with the names of the sire and dam, and the colour (subject to correction within six months of the date of whelping), sex, and number of the puppies. In this way there is in the Greyhound Stud Book of the present day an authentic record of every greyhound born.

From the point of view of accuracy in the present statistics it is unfortunate that colour registration should have to be made at so early an age, for there is no doubt that in many cases colour changes with age, and there may be, in fact are, cases in which the colour would have been registered differently had the date of registration been postponed. There is one other point to which I would draw your attention. Under the heading of "Registration Regulations" there is the following instruction:—

> "It is not desirable to register a colour which is not seen by the judge when following the dogs. Thus it often happens that a black dog has an insignificant patch of white on his chest, it may be a few white hairs on the tip of his tail or a white toe. The entry of such a dog as black and white simply leads to confusion, and should be avoided."

From the practical standpoint this is an excellent rule, but it is not conducive to that accuracy in description which is of such vital importance when dealing with colour from a scientific or statistical point of view.

Bearing these points in mind, I began with the Greyhound Stud Book for the year 1907, and have worked through the fifteen succeeding volumes up to, and including, that published in 1921. In this way the records of 16,260 litters have been examined and the colours of 25,767 whelps have been tabulated. The pigmentary factors of greyhounds resemble those of other animals in that they consist of black, chocolate (known as red), and yellow. In addition, the greyhound has a composite colour known as brindle, which is due to a pattern factor combining with one, or more, of the other colours. The results, generally, may be taken to represent the actual colours of the various individuals, but personal observation shows that there are certain discrepancies. Thus there are blacks, so registered, that show brindle markings, and the returns do not differentiate, in the majority of cases, between red and fawn, the usual description being "red or fawn," which explains why it has been necessary for me to group these two colours together under one heading. Pure albinism of the skin and hair is very rare, but partial albinism is common in the pied patterns. Other colours, or combinations of colours, such as blue-brindle, blue-fawn, black-brindle, etc., are often met with, but these are too ambiguous to be taken into account and are not included in my figures.

Take first the matings of black to black. On the assumption that black and blue are dominant over all other coat colours, the blacks can be of two kinds: pure dominant blacks, containing nothing but black factors, and impure dominant blacks, containing one black factor and one alternative factor, which may be either brindle, or red, or fawn. Now, though pure dominants do occur in all colours, they are rare. Greyhounds are bred for speed and work. Colour is a minor consideration, and of the thousands of dogs born, only a very small percentage of them

ever stand at stud, and, of these, only very few have a sufficient number of mates upon which an assumption of pure dominance could be based. For these reasons it may be taken that the parents concerned in the 500 black to black matings were impure dominants in gametic composition. The 500 matings yielded 3603 whelps, and, on the basis of the classical Mendelian ratio of 3 : 1, the expectation is that there would be 2700 blacks to 900 brindles, red or fawns, and whites. The observed results gave 2697 blacks and blues to 906 brindles, red or fawns, and whites.

In the black to blue matings, of which there were 231, there were 1338 whelps, and the expectation is the same as in the black to black matings: namely, three blacks and blues to one other colour. This would give 1003 blacks and blues to 335 brindles, red or fawns, and whites. The actual results were 998 to 340.

These figures clearly establish the premise that black is the epistatic colour, and is dominant over all others.

Take next the matings of black to brindle. The case here is one of an impure dominant to a recessive, so that the resulting offspring should be an equal number of impure dominants and of recessives. That is to say, there should be an equal number of blacks and blues to brindles, red or fawns, and whites. The number of whelps in the 500 matings was 3053, so that there should have been 1526 of each. The actual result was 1533 blacks and blues to 1520 brindles, red or fawns, and whites.

In the black to red or fawn matings the case is again one of impure dominant to recessive. Again equality would be expected, so that of 3039 whelps there should be 1519 of each. The actual result was 1525 : 1514.

These figures still further conclusively prove that black is epistatic to brindle and to red or fawn.

Take now the blue matings. I have taken up the black to blues. In the blue to brindle matings the case is one of impure dominant to recessive, and the expected result from 1293 whelps would, therefore, be 646 blacks and blues to 646 brindle, red or fawns, and whites. The actual result was 649 : 644.

Blue and red or fawn matings fall into the same scheme, and from 1822 whelps the result should have been 911 : 911, whereas it was actually 915 : 907.

The blue to blue matings only numbered 25, and resulted in 132 whelps. Here the scheme is impure dominant to impure dominant, which should give 3 blues and blacks to 1 brindle, red or fawn, and white. The expected result was therefore 99 blues and blacks to 33 brindles, red or fawns, and whites. The observed result was 93 to 39.

In the table it will be seen that in these matings there were 6 blacks and 1 black and white, and this, or these, raise a difficulty. Blue is undoubtedly a dilute black, and the previous small incidence of blues clearly shows that if there is a special

dilution factor, it cannot be epistatic to the saturation factor. In these circumstances it must be recessive, and being so, there should be no blacks in the blue to blue matings. Very possibly the blacks were dark blues verging on black, but, anyhow, the blue to blue matings are too few to form a reliable guide.

Turning next to the brindle and brindle matings. On the hypothesis that brindle is recessive to black and blue and dominant over red or fawn and white, there should be no blacks or blues from brindle to brindle matings. Theoretically, with the blackness stripped off, the brindles become dominant or, as dominants are rare, impure dominant to the recessive red or fawns and whites. Thus the mating is one of impure dominant to impure dominant, and the expected result from 2829 whelps would be 2121 brindle to 707 red or fawns and whites. The actual result was 30 blacks and blues : 2118 brindles and 681 red or fawns and whites.

The 30 blacks were made up of 14 blacks; 9 black and whites; 6 blues and 1 blue and white. The error of deviation is so small that I think it may be laid down to inaccuracy of description.

In the case of brindle to red or fawn, there were 2932 whelps, and as it was a case of impure dominant to recessive the expectation was that there would be equality or 1466 brindles to 1466 red or fawns and whites. The actual result was 1465 to 1458, but there were, in addition, 9 blacks, which once again, though unsatisfactory, must be attributed to descriptive error.

The last of the more simple results are reached in the matings between red or fawn and red or fawn. On the hypothesis that red or fawn are hypostatic to everything but white, the expectation is that there would be no colours in the 2925 whelps but red or fawns and a few whites. Actually, the figures observed were 10 blacks, blues and brindles: 2910 red or fawns and 5 whites. The incidence of the epistatic colours black, blue, and brindle is so low that one is justified in assuming that their presence in this mating is due to personal error rather than to genetics.

Reviewing the above results, I think I have proved that greyhound coat colours follow the sequence of black, which is epistatic, blue, brindle, red or fawn, and white, which is hypostatic, and that, secondly, blue is a dilute black.

From supplementary statistics I find that there are undoubtedly pure dominants for both black and brindle, and, as I have shown, red or fawns breed true, which is invariably the case with a recessive character. Thus it follows that if such were of any practical use to the coursing man, he would have no difficulty in establishing pure breeding strains of either black, brindle, red or fawn.

I now turn to the secondary results of the matings, and these are somewhat more complicated than the primary data already discussed.

In the black to black matings, if the blacks are taken as impure dominants and of two sorts:

(1) blacks carrying a brindle factor as recessive,

(2) blacks carrying a red or fawn factor as recessive,

and the incidence of both blacks are equally numerous, the ratio arising should be:—black, 12 : brindle, 3 : red or fawn, 1. Further, if every black dog or bitch carried both brindle and red or fawn factors, the incidence would be the same, as red or fawn could only appear in the absence of brindle.

It will be observed that the incidence of black came out correctly in the black to black and blue to blue matings, but in the place of the brindles being in the ratio of three to one red or fawns, the colours are almost equally distributed in the black to black matings, whereas in the blue to blue matings the red or fawns are almost twice as numerous as the brindles. These results cannot be explained by the law of probability, based on the interaction of factors arising out of the hypothesis, already proved, that brindle is dominant over red or fawn.

In the mating of black to brindle, the Mendelian expectation is:—black, 4: brindle 3, red or fawn 1; and the 3053 whelps should therefore give 1526 blacks : 1145 brindles and 381 red or fawns and whites. The observed results gave 1533 blacks and blues: 1018 brindles and 484 red or fawns and whites.

Here the results are sufficiently close—having regard to the fact that the actual incidence of the recessive factors in the DR blacks is unknown—to be taken as in accordance with probability.

On the other hand, the Stud Book returns for black to red or fawn show, as regards the incidence of brindles and red or fawn, a totally unexpected result. In the 3039 whelps the expected result was that there would be 1519 blacks: 789·5 brindles and 789·5 red or fawns; whereas the actual result was 1525 blacks: 492 brindles, and 1007 red or fawn and whites. At the moment the explanation of these figures is beyond me, but I think it is worth noting that in the black to black matings the incidence of brindles and red or fawns is practically equal, and the same holds true in the black to blue matings. In the black to brindle and the black to red or fawn matings there is again a similarity, as in the former the ratio of brindle to red or fawn is as 2 to 1, whilst in the latter the ratio is practically reversed. This may be nothing more than a coincidence of figures, but somehow I think it holds the key to the explanation. My own idea was that black carries a factor which produces either brindle or red according as to the factor introduced by the other parent, but if this were so, in the black to red or fawn matings there should be no brindles, whereas there were actually 492 in 3039 whelps.

In passing to the mixed colours, it is interesting to note that

throughout the series the mixed combinations very generally follow the same incidence of ratio as the whole colours with which they are associated.

Let me now devote a few words to the mixed matings—that is to say, the "pied" colours, in which white plays a leading part on both sides. These unions, on the whole, fall into line with those of melanistic character. One would have expected a higher incidence of whites in these matings, but it is interesting and important to note that in the red or fawn and white to red and fawn and white, the hypostatic colours in the scale, there are more whites than in any other matings. It seems probable that the mixed colours tend to segregate into the conditions of melanism and albinism of the skin and hair, giving 1 whole colour : 2 mixed colours : 1 white. When we recall the instruction concerning the registration of colours, it is self-evident that there is a very appreciable chance that some mixed colours are nearly white. This being so, there should be about 3 "mixed" to 1 whole colour in the pied matings.

Adding the "white" to the "pied" in the whole series, it will be found that the total is 2413 "pied" and white to 689 whole colours, which gives a ratio of 3·5 to 1, which is sufficiently close for all practical purposes.

In conclusion, I must thank Mr. Robertson for all the help he has given me in drawing up this paper and Mr. Martin Duncan, our Librarian, for his kindness in furnishing me with what references on the subject there are.

WHOLE COLOUR MATINGS.

BLACK × BLACK.

Matings. 500.
Whelps. 3603.

Bk. 1607	Be. 196	Bd. 314	R. or F 271	W. 21
BkW. 796	BeW. 98	BdW. 162	R. or FW. 138	
2403	294	476	409	21
	2697		906	
Expectation.	2700		900	

BLACK × BLUE.

Matings. 231.
Whelps. 1338.

Bk. 616	Be. 226	Bd. 112	R or F. 162	W. 7
BkW. 118	BeW. 38	BdW. 32	R or FW. 27	
734	264	144	189	7
	998		340	
Expectation.	1003·5		334	

BLACK × BRINDLE.

Matings. 500.
Whelps. 3053.

Bk.	1115	Be.	123	Bd.	869	R. or F.	395	W. 18
BkW.	258	BeW.	37	BdW.	149	R. or FW.	89	
	1373		160		1018		484	18
		1533				1520		
Expectation.		1526				1526		

BLACK × RED or FAWN.

Matings. 500.
Whelps. 3039.

Bk.	1139	Be.	146	Bd.	400	R. or F.	877	W. 15
BkW.	223	BeW.	17	BdW.	92	R. or FW.	130	
	1362		163		492		1007	15
		1525				1514		
Expectation.		1519				1519		

BLUE × BLUE.

Matings. 25.
Whelps. 132.

Bk.	6	Be.	76	Bd.	12	R. or F.	23	W. —
BkW.	1	BeW.	10	BdW.	1	R. or FW.	3	
	7		86		13		26	
		93				39		
Expectation.		99				99		

BLUE × BRINDLE.

Matings. 213.
Whelps. 1293.

Bk.	369	Be.	175	Bd.	349	R. or F.	189	W. 2
BkW.	73	BeW.	32	BdW.	74	R. or FW.	30	
	442		207		423		219	2
		649				644		
Expectation.		646				646		

BLUE × RED or FAWN.

Matings. 291.
Whelps. 1822.

Bk.	519	Be.	249	Bd.	164	R. or F.	598	W. 6
BkW.	116	BeW.	31	BdW.	50	R. or FW.	89	
	635		280		214		687	6
		915				907		
Expectation.		911				911		

BRINDLE × BRINDLE.

Matings. 500.
Whelps. 2829.

Bk. 14	Be. 6	Bd. 1898	R. or F. 527	W. 18	
BkW. 9	BeW. 1	BdW. 220	R. or FW. 139		
23	7	2118	663	18	
30		2118	681		
Expectation. 0		2121	707		

BRINDLE × RED or FAWN.

Matings. 500.
Whelps. 2932.

Bk. 9	Be. —	Bd. 1343	R. or F. 1287	W. 4	
BkW. —	BeW. —	BdW. 122	R. or FW. 167		
9	—	1465	1454	4	
9		1465	1458		
Expectation. 0		1466	1466		

RED or FAWN × RED or FAWN.

Matings. 500.
Whelps. 2925.

Bk. 2	Be. 2	Bd. 1	R. or F. 2560	W. 5
BkW. 4	BeW. 1	BdW. —	R. or FW. 350	
6	3	1	2910	5
10			2910	5
Expectation. 0			2920	5

MIXED COLOUR MATINGS.

BLACK and WHITE × BLACK and WHITE.

Matings. 100.
Whelps. 532.

Bk. 92	Be. 16	Bd. 24	R. or F. 32	W. 4
BkW. 280	BeW. 12	BdW. 56	R. or FW. 16	
372	28	80	48	4
400			132	
Expectation. 399			133	

BLACK and WHITE × BRINDLE and WHITE.

Matings. 100.
Whelps. 552.

Bk. 48	Be. 16	Bd. 64	R. or F. 44	W. 4
BkW. 176	BeW. 32	BdW. 116	R. or FW. 52	
224	48	180	96	4
272			280	
Expectation. 276			276	

BLACK and WHITE × RED or FAWN and WHITE.

Matings. 100.
Whelps. 564.

Bk. 72	Be. 10	Bd. 22	R. or F. 52	W. 22	
BkW. 184	BeW. 14	BdW. 78	R. or FW. 110		
256	24	100	162	22	
	280		284		
Expectation.	282		282		

BLUE and WHITE MATINGS too few to be used.

BRINDLE and WHITE × BRINDLE and WHITE.

Matings. 100.
Whelps. 430.

Bk. —	Be. —	Bd. 50	R. or F. 34	W. 5
BkW. —	BeW. —	BdW. 270	R. or FW. 71	
—	—	320	105	5
		320	110	
Expectation.		321	107	

BRINDLE and WHITE × RED or FAWN and WHITE.

Matings. 100.
Whelps. 502.

Bk. 8	Be. 8	Bd. 32	R. or F. 68	W. 20	
BkW. 14	BeW. 4	BdW. 220	R. or FW. 128		
22	12	252	196	20	
		252		216	
Expectation. 0	0	251		251	

RED or FAWN and WHITE × RED or FAWN and WHITE.

Matings. 100.
Whelps. 631.

Bk. —	Be. —	Bd. —	R. or F. 53	W. 62
BkW —	BeW. 1	BdW. 2	R. or FW. 513	
—	1	2	566	62
Expectation. 0	0	0	569	62